Colour Coding in LGN and V1 revealed by fMRI pattern classification

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Introduction The application of pattern classification algorithms to look at brain activation patterns produced by fMRI is an exciting new development which has recently confirmed the presence of orientation tuning in the human visual cortex (1,2). In this work a similar approach is used to investigate chromatic tuning at different levels of the visual processing stream, from the Lateral Geniculate Nucleus (LGN) to the primary visual cortex areas V1 and V2. It is known that different layers of cells in the LGN are highly tuned to three colour directions (3,4): black-white, red-green and yellow-violet. We refer to these as 'LGN-colours'. Tuning in V1 or higher areas is unclear (5-7), but might be expected to align more closely with what we perceive as focal colours, i.e. red, green, yellow and blue. We refer to these as 'perceptual-hues'. In this study the LGN is used as a test system where we expect that LGN-colours will produce different activation patterns and so will show high classification performance. The success of classification of fMRI activation patterns in higher visual areas will determine the degree of tuning to LGN-colours in these areas. A second experiment using perceptual-hues tests whether higher visual areas respond preferentially to these.

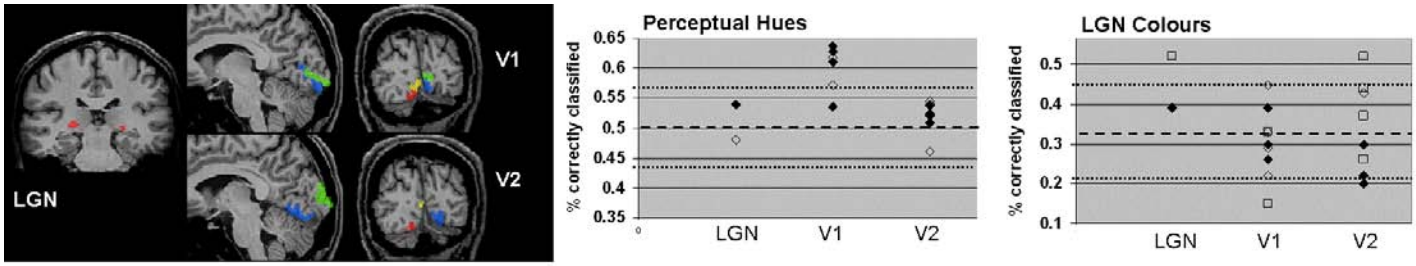
Methods

Visual Stimuli: Experiments were run on a standard PC with a VSG2/5 graphics card (32-MB memory, Cambridge Research Systems, Ltd.). Stimulus presentation was controlled with Matlab 7 (Mathworks®) and stimuli were presented on a PANASONIC LCD PT-L785U, which was calibrated using a spectroradiometer (Photo Research PR650). In session 1, we used colour directions that are known to differentially stimulate neurons in the Lateral Geniculate Nucleus (4,5'LGN-colours'). The CIE xy coordinates of these three colour modulations were as follows. The red-green direction varied from x=0.408,y=0.402 (reddish) to x=0.324, y=0.459 (greenish); the yellowish-violet direction from x=0.418, y=0.538 (yellowish) to x=0.336,y=0.357 (violet). All colour stimuli were presented on a grey background (x=0.369, 0.429) of the same luminance (470 cd/m^2). The third direction was achromatic (ranging from black to white) with the same chromaticities as the grey background and only the luminance varied. The overall contrasts (= vector length in cone contrast space) for the red-green, yellow-violet and black-white modulations were 8%, 80% and 60%, respectively. These contrasts were chosen such that they produced roughly similar cortical BOLD responses (6). In session 2, 'perceptual hues' were used. For each observer the perceptual hues (i.e. red, green, yellow, blue) were assessed individually prior to the scan using a hue-cancellation task (7). The contrast of the perceptual hues was then scaled such they were roughly equal in terms of detectability (10). Stimuli were now modulated between the grey background colour and a particular perceptual hue. All perceptual hues had the same luminance as the grey background (100 cd/m^2).

Procdedure&Task: Stimuli were presented in a block design. Each block lasted 12s. The control block was neutral grey background. The stimulus block was a flickering radial sinusoidal grating (0.8 cycles/deg; 1.5 Hz) presented on the same neutral grey background, similar to that used in (6). To control for attention subjects were asked to perform a forced choice task throughout the experiment where they had to decide if the fixation shape was a circle or a square.
Session 1: LGN-colours: The 3 LGN-colour stimuli were presented 3 times each in a random order per run (216s). There were 6 runs. 3 subjects took part.
Session 2: Perceptual Hues: The 4 perceptual-hues were presented 3 times each in a random order per run (288s). There were 5 runs. 2 subjects took part.
Retinotopic mapping: A rotating 8Hz flickering 45 degree wedge was presented. There were 10 rotations with one rotation lasting 48s.
MRI methods: All scanning was performed on a 3 T Siemens Trio system. High resolution EPI with prospective motion correction was used with scan parameters: TR 3s, TE 35ms, matrix 128x128, in-plane resolution 1.5mm, slice thickness 2mm, 29 slices covering the occipital cortex. A 1mm isotropic structural image was collected.

Analysis: Retinotopic maps were produced using BrainVoyager and thresholded to FDR level p=0.05. Visual areas defined according to (8). The LGN region was defined as the area in the thalamus that was significantly activated (p=0.05, uncorrected) during the colour stimulus. The 4 quadrants of both V1 and V2, and the LGN region were each used as binary masks for the later analysis. The fMRI data from the colour runs was carefully aligned to the structural scan of each individual subject using BrainVoyager. Motion correction, slice time correction and linear trend removal (but no spatial or temporal smoothing) was applied. For each colour stimulus the data 7 to 15s following the start of the colour block was averaged and the 6s preceding the colour block was subtracted, resulting in a single image for each colour stimulus. Support Vector Machines (9) were used to classify the fMRI activation patterns according to the colour stimulus applied within the mask of each visual area. A leave-one-out approach was used iteratively to give the same number of classification results as there were colour conditions. For example, the LGN-colour session had 18 presentations of each of 3 colour stimuli; 54 images in total. The SVM is trained on 53 images and tested on the remaining image. This is repeated until all of the images have been tested, giving 54 classification results for each region of interest.

Results and Discussion



The figure on the left shows the four quadrants of V1 and V2 along with the LGN region as defined for a typical subject. On the right are the results of the classification of the data within these regions across all subjects. Each subject is represented by a different symbol. The dashed line represents chance performance and the dotted lines the 95% confidence interval on this null hypothesis of chance performance. For the perceptual-hues, pairwise classification was performed between all colour pairs, with chance performance at 50% as shown by the dotted line. It can be seen that LGN data is not classified better than chance, whereas V1 data in all quadrants of both subjects was consistently classified better than chance. The V2 data shows poorer classification than V1 but 7 out of 8 regions are classified better than chance, although not within the 95% confidence interval. For the LGN-colours classification was performed between 3 colour conditions, hence chance is now 33%. In this case neither V1 nor V2 data is correctly classified, but both sets of LGN data are classified better than chance.
These results suggest that the LGN has cells that are tuned to the LGN-colour directions, as expected. More subjects need to be scanned to confirm this finding. The data in V1 shows no classification for the LGN-colours but significant classification for the perceptual-hues suggesting that V1 cells are tuned to these colours.

References 1. Haynes and Rees 2005 2. Kamitani and Tong 2005 3. De Valois and Jacobs 1968 4. Derrington et al 1984 5. De Valois et al 2000 6. Liu and Wandell J Neurosci, 2005. 7. Wuerger et al 2005. 8. Wandell et al, 2005. 9. Joachims http://svmlight.joachims.org/. 10. Webster et al., JOSA, 2000.